Stable Isotopes in Aquatic Systems: Sample Preparation, Analysis, and Interpretation

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STABLE ISOTOPES IN AQUATIC SYSTEMS: SAMPLE PREPARATION, ANALYSIS, AND INTERPRETATION

by

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ABSTRACT

This report was written to provide background information for aquatic ecologists interested in using stable isotope analysis (SIA). Ratios of stable isotopes of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and sulphur ($^{34}S/^{32}S$) differ among various substances, and allow for dietary inferences to be made due to the predictability of isotopic relationships between consumers and their food. SIA has been used to construct food webs in streams, lakes, estuaries, and oceans. SIA also has been employed to examine contaminant bioaccumulation in top predators, to identify migrant individuals, and to quantify nutrient sources and their uptake. Potential problems exist, however, that require a researcher's awareness, to avoid potentially erroneous and misleading interpretation of data. SIA is becoming a powerful tool in ecology due to its integrative nature and its potential for non-destructive sampling.

RÉSUMÉ

Ce rapport fut écrit afin de fournir des connaissances de base aux écologistes aquatiques intéressés d'effectuer l'analyse des isotopes stables (AIS). Les rapports des isotopes stables du carbone ($^{13}C/^{12}C$), azote ($^{15}N/^{14}N$), et soufre ($^{34}S/^{32}S$) diffèrent parmi plusieurs substances et permettent de déduire l'alimentation par la prédictibilité des relations isotopiques entre les consommateurs et leur nourriture. AIS a été employée afin d'établir la chaîne alimentaire dans les ruisseaux, lacs, estuaires et océans. AIS a également été utilisée pour examiner la bioaccumulation des contaminants chez les prédateurs supérieurs, identifier les individus migrateurs, et quantifier les sources et la consommation des nutriments. Néanmoins, les chercheurs doivent être informés de l'existence de problèmes potentiels afin d'éviter l'interprétation erronée ou trompeuse des données. AIS devient un outil puissant en écologie par sa nature intégrée et son potentiel pour l'échantillonnage non-destructif.

INTRODUCTION

Stable isotope chemistry

Certain elements in nature exhibit variations in atomic weight based on differences in the number of neutrons in the nucleus. This does not affect their general physical or chemical properties, but does allow for their identification by isotope ratio mass spectrometry (IRMS), as all substances carry a unique signature (proportion) of given variable forms. These mass unit variations of elements are known as isotopes, and those that do not decay over time (non-radioactive) are termed stable (Schimel 1993). Stable isotope science, traditionally used as a tool in geo-chemical studies, has become an increasingly useful method for quantifying energy flow in ecosystems. The utility of stable isotopes is in their ability to record both source (equilibration) and process (fractionation) information (Peterson and Fry 1987).

The three main elements used in stable isotope analysis (SIA) for ecological research are carbon, nitrogen, and sulphur. Carbon exists primarily as the carbon-12 isotope (98.89%), but a small fraction (1.11%) is present as carbon-13, while nitrogen's most abundant form is the nitrogen-14 isotope (99.64%), with nitrogen-15 making up the remainder (0.36%). Sulphur exists in four stable forms. Sulfur-32 is the most common (95.02%), but contributions to total sulphur are also made from sulfur-34 (4.21%), sulphur-33 (0.75%), and a small fraction from sulfur-36 (0.02%). Many other elements, including hydrogen and oxygen, also have multiple stable forms that lend themselves to analysis, but are not considered here.

The different isotopes, while possessing the same fundamental chemical properties, differ in characteristics that are a direct consequence of their atomic mass, such as gas density, condensed phase density, and rates of diffusion and evaporation. Another major difference between isotopic forms is their thermodynamic characteristics, properties that cause reactions in biochemical processes to occur at slightly different rates (Urey 1947). These differences in rate will favour either the lighter or heavier isotope, leading to depletion or enrichment, respectively, of the product relative to the substrate (or the consumer relative to its energy source).

International isotopic standards

In order to accurately compare isotopic values across experimental studies, various standards were developed for individual isotopes. These standards were originally chosen because they demonstrated consistent values (in isotope %) after multiple measurements. Craig (1957) used carbon dioxide from calcium carbonate produced by a cretaceous belemnite, *Belemnitella americana*, from the Peedee formation of South Carolina (PDB) as a standard for $\delta^{13}C$, and this has since been upgraded to a Vienna PDB (VPDB) scale by assigning a fixed value of 1.95‰ to National Bureau of Standards (NBS)-19 calcite (Coplen 1996). Standards originally used for nitrogen and sulphur were atmospheric nitrogen (AIR) (Mariotti 1983) and Canyon Diablo troilite (of meteoric origin) (CDT, Thode et al. 1961), respectively. While AIR is still accepted as a

reliable standard for nitrogen measurements, the development of a Vienna CDT (VCDT) scale using a value of -0.3‰ for silver sulphide reference material IAEA-S-1 (International Atomic Energy Agency) has supplanted the use of CDT in sulphur measurements due to CDT's high variability (± 0.4‰, Coplen and Krouse 1998).

Sample calculation

IRMS data are reported as δX values (where X represents the heavier isotope ^{13}C, ^{15}N, or ^{34}S), or differences from the given standards, expressed in parts per thousand or permil (‰), and are calculated according to the formula:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where (using carbon as an example) $R_{sample} = {}^{13}C/{}^{12}C$ of the sample, and $R_{standard} = {}^{13}C/{}^{12}C$ of PDB. R represents the ratio of the abundance of the ions of mass 45 ($^{13}C^{16}O^{16}O$ + $^{12}C^{16}O^{17}O$) to mass 44 ($^{12}C^{16}O^{16}O$); thus a correction factor for ^{17}O is required (Craig 1953). Similar calculations can be performed comparing samples and standards for nitrogen [$R = {}^{15}N/{}^{14}N$, as measured by the ratio of the abundance of ions of mass 29 ($^{14}N^{15}N^{+}$) to mass 28 ($^{14}N^{14}N^{+}$) (Mariotti 1984)], and sulphur [($R = {}^{34}S/{}^{32}S$, as measured by the ratio of the abundance of ions of mass 66 ($^{34}S^{16}O^{16}O$ + $^{32}S^{18}O^{16}O$) to mass 64 ($^{32}S^{16}O^{16}O$). Therefore, correction must be made for ^{18}O (as opposed to ^{17}O) in sulphur analysis (Holt and Engelkemeir 1970, Fry et al. 2002)].

The use of ratios allows for large discrepancies (in ‰) to be observed between samples that differ only slightly in the percentage composition of given isotopes (Peterson and Fry 1987). This largely increases resolving power and permits comparisons across analytical laboratories and studies.

Isotope literature

Many excellent textbooks and review papers dealing with stable isotope science have been written (e.g. Peterson and Fry 1987, Rundel et al. 1989, Lathja and Michener 1994, Clark and Fritz 1997, and Kendall and McDonnell 1998), and go into greater detail on specific topics that are only briefly mentioned here.

Carbon flow in a variety of aquatic ecosystem scales is discussed in comprehensive review papers by Fry and Sherr (1984), Rounick and Winterbourne (1986), and Finlay (2001). Other reviews dealing with stable isotopes include: patterns of nitrogen in the marine environment (Owens 1987), nitrogen pollution in air and water (Heaton 1986), food webs in rivers (Woodward and Hildrew 2002), avian and mammalian trophic ecology (Kelly 2000), identification of migrant individuals (Hobson 1999), and applications of stable isotopes in understanding physiological processes (Griffiths 1991).

SAMPLE PRESERVATION AND PREPARATION

Due to the small amounts of sample material used in SIA there is high risk of sample contamination. Precautions should be taken while handling specimens to be submitted for analysis (i.e. clean containers, aseptic techniques). Scintillation vials, Eppendorf tubes, vacutainers and whirl pack bags are some examples of containers used for sample collection.

Preservation methods

Freezing specimens and/or tissues collected in the field is the ideal method for sample preservation. No differences were measured between frozen and freeze-dried samples (Bosley and Wainright 1999), so either method is acceptable. For plankton samples, water collected in the field can later be filtered on pre-combusted glass-fibre (or other inorganic) filter papers that have no effect on SI ratios (Hobson et al. 1997).

Other preservation techniques have some major or minor problems. Deleterious effects of formalin on isotope ratios (Hobson et al. 1997, Bosley and Wainright 1999) may be negligible (Junger and Planas 1994) or predictable (Sarakinos et al. 2002). Non-dietary carbonates, such as found in many shellfish species, may affect $\delta^{13}C$, but can be removed by acidification (DeNiro and Epstein 1978). Treatment with hydrochloric acid, however, adversely affects $\delta^{15}N$ (Bunn et al. 1995, Pinnegar and Polunin 1999), so researchers may choose to split tissues into acid-treated and intact sub-samples for separate analyses of $\delta^{13}C$ and $\delta^{15}N$ (Pinnegar et al. 2001). Lysis buffer solutions and dimethyl sulphoxide (solutions typically used to preserve samples for genetic analyses) impact carbon and nitrogen SI ratios (Hobson et al. 1997, Bosley and Wainright 1999), and are therefore not recommended. Instead, ethanol is a preservative that does not appear to affect SI ratios (Hobson et al. 1997).

Submitting samples for analysis

Samples must be sufficiently dried until the tissue can be ground into a fine powder (e.g. 60˚C for 48 hours or freeze-drying). A mortar and pestle, or a ball-mill grinder, may be used to grind the sample into a homogeneous fine powder.

Samples are combusted under high vacuum in small tin capsules. Recent advances in mass spectrometry have resulted in less tissue required for analysis. The exact amount of material is dependent on the concentration of carbon, nitrogen, and/or sulphur in the sample, and the sensitivity of the mass spectrometer used. Typically C and N data can be obtained simultaneously by using a helium diluter (an inert gas used to carry the sample through the system), bringing the carbon peak to a similar amplitude as that of nitrogen (nitrogen being far less abundant in organic materials). For example, tissues with a C:N ratio in the range of 3-6 (e.g. fish muscle, most invertebrates) require approximately 0.2-0.4 mg of dried sample and a dilution of ~15 psi helium to obtain both the C and N isotope data. Whereas 2.0-4.0 mg of tissue may be required if the C:N ratio is closer to 15 (e.g. some plant material), to have an adequate amount of nitrogen in the

sample. The large amount of carbon must then be diluted using ~22 psi helium to obtain data for both elements. For those samples with extremely high C:N ratios where carbon dilution is inadequate, separate analyses may be required to obtain both C&N data. The sulphur content of aquatic species is also highly variable, ranging from 0.1% to 9.0% (Mekhtiyeva et al. 1976), being highest in marine organisms. Hence the range of required sample sizes is equally variable (2.0-15.0 mg).

Ideally, five times the amount of tissue required for a single analysis should be submitted to a lab. This allows for replicate samples that may be needed in case of technical problems, and serves as an indicator of instrumental precision within runs. It is also recommended that a single sample of a common specimen be included in each run to act as an "internal standard", allowing for comparisons across runs.

Additional techniques

Lipid extraction & normalization

The lipid content (which can be estimated from C:N ratio) of a tissue can have a large impact on $\delta^{13}C$ values (McConnaughy and McRoy 1979, Tieszen et al. 1983, Rau et al. 1992, Focken and Becker 1998); consequently many researchers choose a lipid-extraction method such as chloroform-methanol (Bligh and Dyer 1959) or hexane-isopropanol (Radin 1981) prior to analysis. This serves as a form of standardization across samples with unequal lipid content. In lieu of lipid extraction, some workers "lipid normalize" data with high C:N ratios (> 4.0) (Rau et al. 1992, Kline et al. 1998, Kline 1999, Kline and Willette 2002), using a formula:

$$\delta'^{13}C = \delta^{13}C + 6\{-0.207 + 3.9/[1 + 287(1 + 1/(0.246C:N - 0.775))/93]\}$$

that was first presented by McConnaughy and McRoy (1979), where $\delta'^{13}C$ is the lipid corrected stable carbon ratio.

Gut content analysis

While SIA is effective at integrating long-term assimilation of nutrients, it may not necessarily reflect short-term feeding patterns (Persson and Hansson 1999, Johannsson et al. 2001, Hart and Lovvorn 2002). It is recommended that whenever possible, SIA should be combined with gut content analysis (Rau et al. 1983, Mihuc and Toetz 1994, Whitledge and Rabeni 1997, Beaudoin et al. 1999, Johannsson et al. 2001, Grey et al. 2002, Renones et al. 2002). The two techniques, in tandem, can be complementary (Yoshioka et al. 1994, Vaz et al. 1999, Davenport and Bax 2002, Grey et al. 2002) and will likely aid in interpretation of processed data (Evans-White et al. 2001, Parkyn et al. 2001).

INTERPRETATION OF STABLE ISOTOPE DATA

Fractionation

A consumer's stable isotope ratios are relatively accurate reflections of the assimilated portion of its diet. However, as energy transfer occurs in biological systems, isotopic fractionation (change) takes place, resulting in alterations of the consumer's tissue ratios relative to its energy source.

O'Leary (1988) defined isotope fractionation by the equation:

$$\Delta\delta = \frac{[\delta^* X(A) - \delta^* X(B)]}{1 + \delta^* X(A)/1000}$$

where $\Delta\delta$ is the change in isotope ratio that occurs in the reaction from substrate A to product B, and δ^*X(A) and δ^*X(B) are the corresponding stable isotope ratios. This value will have a positive sign when the heavier isotope is transformed more slowly.

Mariotti et al. (1981) described isotope fractionation as "partition of isotopes between two compounds containing the same element (or between two phases) with different isotopic ratios." The authors generated fractionation factors (ε) to express the expected difference (in ‰) between the product and the substrate from which it is formed.

Hobson and Clark (1992a) defined fractionation as changes in isotopic signal between diet and consumer tissues, occurring by two processes: 1) selective biochemical assimilation of dietary components with varying signatures, and 2) isotopic discrimination. The authors used the function:

$$D_t = D_d + \Delta_{dt}$$

to describe the process, where D_t is the isotopic signature of consumer tissue, D_d is the isotopic signature of the diet, and Δ_{dt} is the fractionation factor.

Animal SI ratios relative to diet

Laboratory experiments with animals initially defined the relationship between the carbon and nitrogen isotope ratios of diet and consumer. DeNiro and Epstein (1978) raised a variety of species on homogenous diets of known isotopic composition, and found animal tissue carbon to be ^{13}C enriched roughly 1‰ relative to the diet (avg. = $^{+}$0.8 ± 1.1‰, range = -0.6 to $^{+}$2.7‰). This enrichment can be negligible in some species (Haines and Montague 1979, Focken and Becker 1998, Post 2002), and varies across ecosystems (del Giorgio and France 1996, France and Peters 1997, Vander Zanden and Rasmussen 2001). Freshwater consumers (0.2‰) tend to be less enriched relative to diet than estuarine (0.5‰), coastal (0.8‰), and open-ocean (1.1‰) consumers (France and Peters 1997).

Consumer nitrogen, meanwhile, tends to be ^{15}N enriched by roughly 3-5‰ relative to diet (avg. = $^{+}3.0 \pm 2.6$‰, range = -0.5 to $^{+}9.2$‰, DeNiro and Epstein 1981, Minagawa and Wada 1984). This enrichment is variable across species and systems (Vander Zanden and Rasmussen 2001), but in a broader context has been demonstrated to be fairly consistent in both lab and field (Post 2002).

One exception to the accepted isotopic relationships between consumer and consumed (increasing amounts of tissue ^{15}N at increasing trophic levels) may be aquatic parasite-host associations. These trophic links have been relatively unstudied, and have yielded ambiguous results (Doucett et al. 1999a, Iken et al. 2001, Pinnegar et al. 2001, Deudero et al. 2002), possibly due to differential tissue and nutrient selectivity and metabolism of different parasite species.

Mechanisms responsible for fractionation

Biochemical processes are largely responsible for the fractionation effects measured in animal species. Respiration of carbon dioxide that is ^{13}C-depleted relative to the animal (DeNiro and Epstein 1978, Perkins and Speakman 2001) may explain slight ^{13}C enrichment in animals relative to their diet (DeNiro and Epstein 1978). Discrimination against the heavier isotope (^{13}C) during pyruvate oxidation in lipogenesis (DeNiro and Epstein 1977) results in lipid tissue becoming ^{13}C-depleted. Transamination, wherein transfer of NH_2 from glutamic acid to aspartic acid in an animal's cells proceeds 1.0083 times faster with $^{14}NH_2$ than $^{15}NH_2$ (Macko et al. 1986), is a possible explanation for tissue ^{15}N enrichment during periods of food deprivation. Excretion of isotopically "light" urea and ammonia (Kirshenbaum et al. 1947, Macko et al. 1982, Altabet and Small 1990) is likely responsible for the observed 3-5‰ increase in ^{15}N content at successively higher trophic levels (Minagawa and Wada 1984).

Equilibration with a diet in lab and field: Growth vs. turnover

In an organism that has shifted diet to a food source with a unique isotopic signature, two mechanisms (growth and tissue turnover) exist that contribute to isotopic change. An alteration in isotope ratios during rapid growth can be attributed to a "dilution" of the previous ratio by added tissue of differing isotopic composition, while the second mechanism for isotopic change, metabolic turnover, involves a replacement of old tissue with new, and occurs despite no net growth in the animal.

Due to differences in photosynthetic pathways, terrestrial C_3 and C_4 plants have different $^{13}C/^{12}C$ ratios (-32 to –22‰ and –23 to –9‰, respectively). Using these differences, Tieszen et al. (1983) changed a diet based on C_4 plants (corn) to one of C_3 plants (wheat) and shifted stable carbon isotope ratios of gerbils (*Meriones unguienlatus*) towards that of the new source. In an earlier lab experiment with crabs, Haines and Montague (1979) demonstrated a change in $\delta^{13}C$ values upon a diet switch that reflected the new food sources. Persson and Hansson (1999) determined that three months were required for the isotopic composition of new prey items to be detectable in consumer (roach, *Rutilus rutilus*, perch, *Perca fluviatilus*, and bream, *Abramis brama*) tissue.

Johannsson et al. (2001) observed that the tissue turnover rate of $\delta^{13}C$ was much slower than $\delta^{15}N$ in opossum shrimp, *Mysis relicta*.

Different tissues tend to reflect the new diet's ratios at different rates. Tieszen et al. (1983) found liver carbon turnover occurred most quickly while carbon in hair was replaced most slowly. Differential tissue turnover rates were also observed by Hobson and Clark (1992b), who ranked turnover rates in Japanese quail (*Coturnix japonica*) as follows: liver>blood, muscle>>bone collagen. The authors calculated carbon half-lives for liver (2.6 days), blood (11.4 days), muscle (12.4 days), and bone collagen (173.3 days).

Slow metabolic turnover rates in ectotherms (due to lower energy requirements relative to endotherms) may explain the greater influence of growth on isotope changes in species such as broad whitefish (*Coregonus nasus,* Hesslein et al. 1993), mysids (Gorokhova and Hansson 1999), red drum larvae (*Sciaenops ocellatus*, Herzka and Holt 2000), goby (*Rhinogobius* sp., Maruyama et al. 2001a), brown shrimp (*Penaeus aztecus*, Fry and Arnold 1982, Gleason 1986), larval krill (*Euphasia superba*, Frazer et al. 1997), and winter flounder (*Pseudopleuronectes americanus*, Bosley et al. 2002).

Tissue $\delta^{13}C$ of recently emerged Atlantic salmon (*Salmo salar*) in streams bears a marine signature (-20 to –21.8‰) that is derived maternally from the female returning from the ocean. After a short but rapid period of summer growth (< 2 months) isotopic dilution causes tissue $\delta^{13}C$ to closely mirror local food sources (-24.6 to -27‰) (Doucett et al. 1996a). Smallmouth bass (*Micropterus dolomieu*, Vander Zanden et al. 1998), brook trout (*Salvelinus fontinalis*, Doucett et al. 1999b), and brown trout (*Salmo trutta*, McCarthy and Waldron 2000) have a maternally derived ^{15}N content (enriched) upon hatching, but this signal is rapidly diluted during early growth on a diet consisting of prey from low trophic levels.

Endothermic animals, with higher metabolic demands, are capable of showing altered isotope ratios due to metabolism alone (Tieszen et al. 1983). In ectotherms, the effects of metabolism on isotopic alterations may be significant in older, slower-growing animals (Hesslein et al. 1993).

FOOD WEBS

The predictable relationships between animals and their diet for $\delta^{13}C$ (0-1‰ difference) and $\delta^{15}N$ (3-5‰ difference) (DeNiro and Epstein 1978, 1981) has made possible the study of food webs using stable isotopes (McConnaughy and McRoy 1979, Rau et al. 1983, Minagawa and Wada 1984). Generalized food web structure has been described for freshwater (Figure 1, Estep and Vigg 1985, Fry 1991, Yoshioka et al. 1994, Zohary et al. 1994, Keough et al. 1996, Fry et al. 1999, Vander Zanden et al. 1999a, Yoshii et al. 1999, Harvey and Kitchell 2000, Beaudoin et al. 2001, Fisher et al. 2001, Jepsen and Winemiller 2002, Woodward and Hildrew 2002), estuarine (Peterson et al. 1985, 1986, Kwak and Zedler 1997, Fantle et al. 1999, Hughes et al. 2000), and marine

(Rau et al. 1981, Fry 1988, Hobson and Welch 1992, Rau et al. 1992, Hansson et al. 1997, Ian Perry et al. 1999, Davenport and Bax 2002) ecosystems.

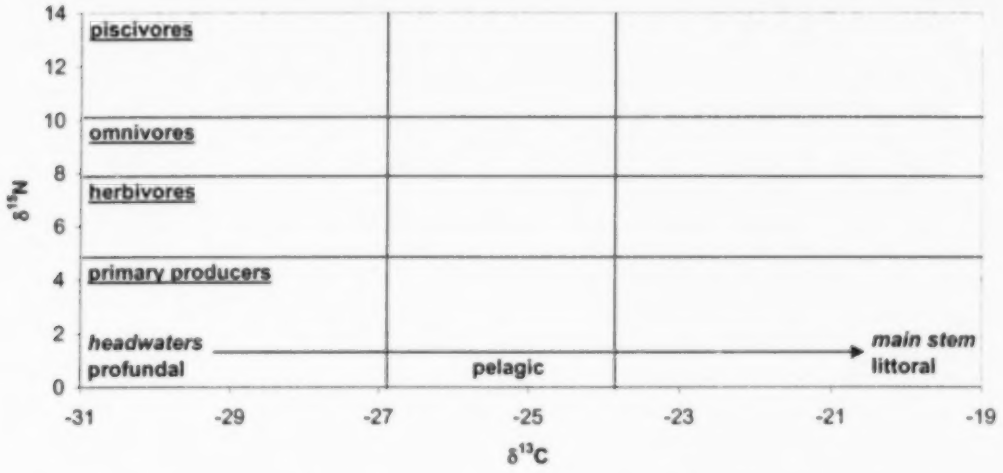

Figure 1. Generalized dual isotope plot ($\delta^{13}C$ and $\delta^{15}N$) for biota in freshwater ecosystems (lakes and streams). Ranges were arbitrarily generated based on Estep and Vigg (1985), Fry (1991), Keough et al. (1996), Vander Zanden and Rasmussen (1999), Harvey and Kitchell (2000), Beaudoin et al. (2001), Fisher et al. (2001), Jepsen and Winemiller (2002), and do not encompass all observed literature values.

Larger scale patterns, such as $\delta^{13}C$ depletion towards polar extremes (Rau et al. 1991), have also been noted. Reconstructions of fisheries abundance and trophic interactions (Badalamenti et al. 2002, Pinnegar et al. 2002) have been aided by paleoecological techniques (Finney et al. 2002, Struck et al. 2002) and analysis of archived scale collections (Wainright et al. 1993, Satterfield and Finney 2002, Struck et al. 2002).

Primary productivity

Stable isotope signatures at the base of food webs in estuaries (Cifuentes et al. 1988, Middelburg and Nieuwenhuize 1998, Cloern et al. 2002), lakes (Kling et al. 1992, France 1995a, Grey and Jones 1999, Leggett et al. 1999, Owen et al. 1999a), and the marine environment (Rau et al. 1991, Ishihi et al. 2001, Vizzini et al. 2002, Anderson and Fourqurean 2003) can be highly variable (Rau 1980, Gu et al. 1994, Zohary et al. 1994, Kline 1999, Leggett et al. 2000). Stable carbon ratios of primary producers can be a function of chlorophyll a, phosphorus, and carbon dioxide concentrations (Yamamuro et al. 1995, Gu et al. 1996a, Leggett et al. 1999), light intensity and water velocity (Osmond et al. 1981, MacLeod and Barton 1998, Finlay et al. 1999), upwelling, bloom, and flood events (Estep and Vigg 1985, Bode et al. 2003), and dissolved organic (France 1999, France 2000, Burd et al. 2002), inorganic (Keough et al. 1998), and bacterial (Van Dover and Fry 1994, Hall and Meyer 1998) carbon sources.

Boundary layer diffusion (the flow of dissolved gases in the medium surrounding an organism) of carbon dioxide influences isotopic fractionation during photosynthesis. Benthic algae are CO_2 limited, and therefore cannot preferentially take up the lighter isotope ($^{12}CO_2$). Planktonic algae are surrounded by an abundance of available CO_2, and therefore can discriminate against the heavier isotope ($^{13}CO_2$). Thus, benthic algae are enriched in ^{13}C relative to planktonic algae (France 1995a, Hecky and Hesslein 1995), and the differences are passed on to consumers (France 1995b).

Variation in the ^{15}N content of organisms at the base of lake food webs (Gu et al. 1994) will influence the interpretation of trophic level of species higher in the food chain. Comparison of trophic levels across lakes using $\delta^{15}N$ (Cabana and Rasmussen 1994) has been aided by measuring the stable nitrogen ratios of long lived primary consumers such as unionid mussels (*Lampsilis* sp., *Anodonta* sp., and *Elliptio* sp., Cabana and Rasmussen 1996, Vander Zanden et al. 1997, Vander Zanden and Rasmussen 1999) and clams (*Potamocorbula amurensis*, Fry 1999) that integrate temporal variability of planktonic isotope ratios into a baseline signal.

APPLICATIONS

Contaminants

The knowledge that the $\delta^{15}N$ of higher predators represents an integration of trophic levels over the life span of the organism has enabled researchers to correlate $\delta^{15}N$ with tissue concentrations of contaminants such as mercury (Cabana and Rasmussen 1994, Jarman et al. 1996, Atwell et al. 1998, Bowles et al. 2001, Power et al. 2002a) and organochlorines (Spies et al. 1989, Kidd et al. 1995, Kiriluk et al. 1995, Jarman et al. 1996, Kucklick et al. 1996, Kidd et al. 1998). Using such relationships, predictive models have been developed where invasive species have caused longer food chains and higher contaminant body burdens in top predators (Cabana and Rasmussen 1994, Swanson et al. 2003). However, in some situations trophic level (as measured by $\delta^{15}N$) has had limited power in explaining variability of mercury concentrations relative to other environmental variables such as pH (Greenfield et al. 2001). Other factors that can influence the relationship between $\delta^{15}N$ of higher predators and lipophilic contaminant concentrations include carbon sources (Power et al. 2002a) and uptake and clearance rates of the contaminant (Broman et al. 1992).

Migratory patterns

Freshwater and marine nutrients have distinct carbon (Craig 1953, Peters et al. 1978), nitrogen (Peters et al. 1978, Owens 1987), and sulphur (Mekhtiyeva et al. 1976) isotope signatures (marine systems generally have higher amounts of the heavier isotopes, Peterson and Fry 1987). Species that derive biomass from the different environments will have correspondingly different stable isotope signatures, allowing for the identification of migrant individuals. Anadromous Arctic charr (*Salvelinus alpinus*), brown trout, and brook trout were identified by marine carbon (Bunn et al. 1989, Doucett et al. 1999b, 1999c, McCarthy and Waldron 2000), nitrogen (Doucett et al. 1999b,

1999c, McCarthy and Waldron 2000), and sulphur (Doucett et al. 1999b, 1999c) signatures. Marine and freshwater feeding has also been distinguished for broad whitefish and Arctic cisco (*Coregonus autumnalis*, Hesslein et al. 1991, Kline et al. 1998), harbour seals (*Phoca vitulina*, in combination with essential fatty acid analysis, Smith et al. 1996), alosids (*Alosa* spp., in combination with strontium otolith analysis, Limburg 1998, MacAvoy et al. 2000), and a variety of migratory birds (Lott et al. 2003).

Isotopic differences may also exist at smaller scales (regional, local). As long as nutrient sources for consumers are isotopically distinct, then nutrient assimilation can be distinguished and movement patterns identified. For example, isotopic differences identified two populations of catfish (*Silirus biwaensis*, Takai and Sakamoto 1999) and movements by landlocked goby (Maruyama et al. 2001b) in Lake Biwa, wild and released abalone (*Haliotis diversicolor*) in northeastern Taiwan (Lee et al. 2002), and inshore and offshore feeding by seabirds in the northeast Pacific (Hobson et al. 1994). SIA has also been used to demonstrate little migratory activity by young-of-the-year herring (*Clupea harengus*), sprat (*Sprattus sprattus*), smelt (*Osmerus eperlanus*), and pikeperch (*Stizostedion lucioperca*) in the Baltic Sea (Hansson et al. 1997), and the consumption of littoral invertebrates by omnivorous mice (*Peromyscus maniculatus*) on islands in the Gulf of California (Stapp and Polis 2003).

Mixing models

When organisms have two or more sources of energy for growth, mixing models have been employed to determine the relative contribution of the sources. These include marine-derived nitrogen in freshwater food webs from spawning Pacific salmon (*Oncorhynchus* spp., Kline et al. 1990, 1993, Bilby et al. 1996, Ben-David et al. 1997, Figure 2) and alosids (MacAvoy et al. 2000).

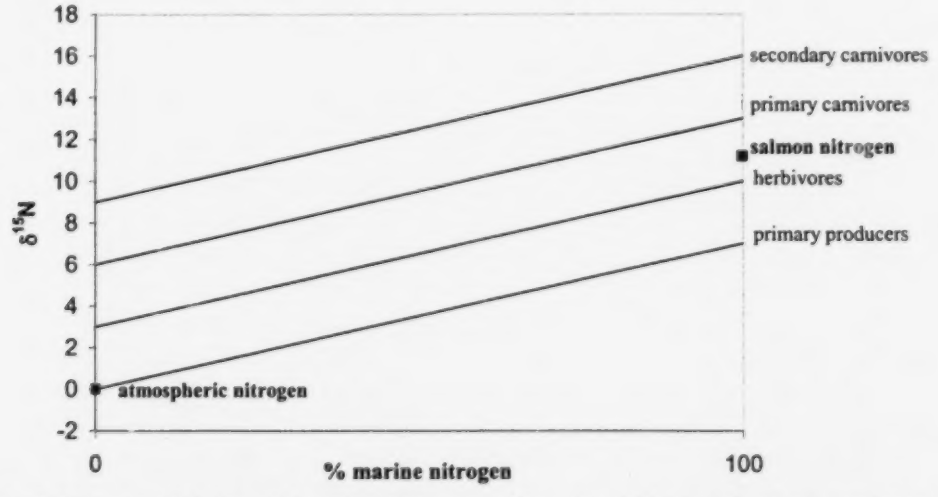

Figure 2. Mixing model describing the influence of marine (salmon) derived nutrients on stable nitrogen ratios within a freshwater food web. Organisms using 100% marine-derived nitrogen are ^{15}N-enriched ca. 7‰ relative to organisms using nitrogen fixed in terrestrial/freshwater systems. Adapted from Kline et al. 1990.

Mixing models have also been used to identify anthropogenic nutrient inputs to riparian food webs (Wayland and Hobson 2001), to estimate the degree of dietary overlap by fishes (Bootsma et al. 1996, Gu et al. 1996b, Genner et al. 1999), and to determine food sources for mayflies (*Baetis* spp., Hershey et al. 1993), crayfish (*Oronectes* sp., Whitledge and Rabeni 1997) and other invertebrates (Hall and Meyer 1998, Hart and Lovvorn 2002).

Multiple-isotope mixing models, however, have been criticized (Ben-David and Schell 2001, Phillips 2001, Phillips and Gregg 2001, Phillips and Koch 2002), due largely to the implicit assumption that organisms obtain equal proportions of bulk carbon and nitrogen from a single food source. Furthermore, mixing models are often not useable because of high variability and overlapping values of food sources (Rosenfeld and Roff 1992, France 1995c).

An oft-studied application of mixing models in freshwater ecosystems is in the analysis of the contribution of allochthonous (terrestrial) and autochthonous (in-stream) nutrients to production (Rau 1980, Palmer et al. 2001, Cloern et al. 2002). Determination of source carbon dependence by stream biota is calculated using the function (Fry and Sherr 1984, Junger and Planas 1994, Doucett et al. 1996a):

$$\%\ \ allochthonous = \left(\frac{\delta^{13}C_{fish} - \delta^{13}C_{autochthonous} - fx}{\delta^{13}C_{allochthonous} - \delta^{13}C_{autochthonous}} \right) \times 100$$

where f is the trophic enrichment factor (typically 0-1‰, DeNiro and Epstein 1978, Post 2002), x is the trophic position of the animal, and $\delta^{13}C_{allochthonous}$ and $\delta^{13}C_{autochthonous}$ are the average stable carbon isotope ratios of terrestrial leaf matter and in-stream algae, respectively.

The contribution of the two sources has been successfully identified for invertebrates (Rounick et al. 1982, Bunn et al. 1989, Junger and Planas 1994, Doucett et al. 1996a, Whitledge and Rabeni 1997, Huryn et al. 2001) and fish (Araujo-Lima et al. 1986, Bunn et al. 1989, Forsberg et al. 1993, Doucett et al. 1996a, Vaz et al. 1999, Benedito-Cecilio et al. 2000, Perry et al. 2003), but high algal variability has led some authors to suggest that the application is site-specific (Rosenfeld and Roff 1992, Zah et al. 2001) and therefore inconclusive (France 1995c, Doucett et al. 1996b, France 1996). The use of two isotopes (e.g. ^{15}N along with ^{13}C) has aided in the interpretation of nutrient sources (France 1997, Collier et al. 2002, Leite et al. 2002).

When the assimilation of nutrients from different sources is unclear, tracer studies involving isotopically labeled (e.g. highly enriched in ^{15}N) compounds may be used. Nitrogen cycling in a tundra river (Peterson et al. 1997), a tropical rainforest (Merriam et al. 2002), a prairie stream (Evans-White et al. 2001), and an estuary (Hughes et al. 2000) have been calculated using this approach. Amino acids may also be isotopically labelled

and fed to organisms to track nutrient incorporation into tissues (Owen et al. 1999b, Hirons et al. 2001, Epp et al. 2002).

Nutrient input

Stable isotopes have been effective at detecting the input and uptake of nutrients in aquatic ecosystems. Marine-derived (oceanic) nutrients carried by anadromous salmon (Kline et al. 1990, Kline et al. 1993, Bilby et al. 1996, Ben-David et al. 1997, Bilby et al. 1998, Fisher Wold and Hershey 1999, Szepanski et al. 1999, Milner et al. 2000, Helfield and Naiman 2001, Chaloner et al. 2002), alosids (Garman and Macko 1998, MacAvoy et al. 2000, 2001), and marine birds (Mizutani and Wada 1988, Stapp et al. 1999) have been shown to provide an energy subsidy in streams, lakes and estuaries, and on islands.

The impact of humans (through nutrient inputs) on the aquatic environment has also been detected using stable isotope signatures. Human sewage is generally enriched relative to the receiving environment (Heaton 1986, Gearing et al. 1991, Lake et al. 2001), and has been implicated in enriching biota in riparian and offshore food webs (Rau et al. 1981, Estep and Vigg 1985, Spies et al. 1989, Van Dover et al. 1992, Wainright et al. 1996, Hansson et al. 1997, Harvey and Kitchell 2000, Wayland and Hobson 2001). Long-lived primary consumers (e.g. unionid mussels) integrate the nitrogen signature in receiving waters (Fry 1999, Lake et al. 2001), and $\delta^{15}N$ values of such primary consumers have been correlated with human population density (Cabana and Rasmussen 1996). Other effluents that have unique isotope signatures include pulp mill effluent (Wassenaar and Culp 1996, Wayland and Hobson 2001), fish offal (Anderson et al. 1999), and aquaculture wastes (Yokoyama et al. 2002, Yamada et al. 2003). Agricultural practices also generate distinct nitrogen and oxygen signatures that can be detected in rivers (Heaton 1986, Peterson et al. 1993, McClelland et al. 1997, Johnston et al. 1999, Chang et al. 2002, Fry et al. 2003). Run-off and leaching of manure into waterways generates nitrate that is ^{15}N-enriched (~8‰) relative to atmospheric nitrogen and synthetic fertilizers (~0‰) (Peterson and Fry 1987, Wassenaar 1995).

Diet shifts

Stable isotopes of nitrogen and carbon can identify shifts in diet from one food source to another throughout a species' life history. SIA has detected ontogenetic diet shifts in brown trout (Grey 2001), dusky grouper (*Epinephilus marginatus*, Renones et al. 2002), brook charr (Power et al. 2002b), opossum shrimp (Branstrator et al. 2000), migrating salmon smolts (Kline and Willette 2002), and deposit-feeding polychaetes (Hentschel 1998), while other researchers have found no evidence of an ontogenetic diet shift (Vander Zanden et al. 1998) despite a positive relationship between fish size and isotopes of nitrogen and carbon (Guiger et al. 2002). Changes in diet and food web structure after species invasions in lakes have also been measured using SIA (Mitchell et al. 1996, Kidd et al. 1999, Vander Zanden et al. 1999b), as well as evidence of cannibalism by trout species (Grey et al. 2002, Harvey et al. 2002) and shifts by island rodents and beetles from terrestrial sources in wet years to marine sources in dry years (Stapp et al. 1999).

Otoliths

Stable isotope microanalysis of fish otoliths can provide a year-by-year account of feeding history (Schwarcz et al. 1998). This technique ca identify spawning stocks (Gao and Beamish 1999, Gao et al. 2001a), distinguish lagoonal vs. oceanic (Dufour et al. 1998) and hatchery vs. wild (Weber et al. 2002) feeding, and determine the influence of temperature on growth (Gao et al. 2001b, Gao and Beamish 2003)

Large-bodied species

The majority of isotope studies in aquatic systems involve smaller-bodied invertebrate and piscine species, although some work has been done on larger-bodied fish, mammals, and reptiles. The trophic ecology of whales (Abend and Smith 1995, 1997, Hobson and Schell 1998, Hooker et al. 2001, Hoekstra et al. 2002), sharks (Fisk et al. 2002), seals (Kurle and Worthy 2001, Kurle 2002), and turtles (Godley et al. 1998, Hatase et al. 2002) has been described using SIA.

FURTHER CONFOUNDING FACTORS

Although some of the potential challenges in stable isotope ecology have been described above, there are other factors that may hamper a researcher's ability to use SIA to describe feeding relationships in the field. Gannes et al. (1997) stated that assuming an animal's measured isotope ratios directly reflect the contribution of food sources to its diet is potentially erroneous for three reasons. These are: (1) variable assimilation efficiencies of dietary components, (2) isotopic fractionation, and (3) differential allocation of nutrients to specific tissues. The authors specifically noted the use of carbohydrates stores as more labile energy sources, leading to a lesser influence of these inputs on final $\delta^{13}C$ in archaeological studies of human remains.

Variation between seasons, sites, species, individuals, and tissues also presents methodological and statistical challenges for stable isotope research (Lancaster and Waldron 2001). Large intraspecific variations have been found in tilapia (*Oreochromis aureus*, Gu et al. 1997), lake trout (*Salvelinus namaycush*, Vander Zanden et al. 2000) and deposit-feeding polychaetes (Hentschel 1998). Seasonal differences in isotope ratios (Lorrain et al. 2002) may be overcome by time-averaging (O'Reilly et al. 2002). While mathematical models have shown that growing and adult animals should show the same isotope ratios (Ponsard and Averbuch 1999), tissue delta values can be affected by energetics (Harvey et al. 2002) and the nutritional quality of the diet (Hobson and Clark 1992a, Fantle et al. 1999).

Tissue differences

Fractionation strongly affects the resultant isotopic composition of differing tissues within an organism. Lipid rich tissues tend to be most ^{13}C-depleted (Tieszen et al. 1983), yet in Lake Ontario biota, $\delta^{15}N$ and % lipid were correlated, but $\delta^{13}C$ and % lipid

were not (Kiriluk et al. 1995). Other research has found negative correlations of $\delta^{13}C$ with C:N ratio (Gu et al. 1996b), percent carcass lipid (Focken and Becker 1998), and red muscle lipid content (Doucett et al. 1999d).

Estep and Vigg (1985) found consistent differences (2-3‰) between muscle and scale $\delta^{13}C$ in both cui-ui (*Chasmistes cujus*) and Tahoe sucker (*Catostomus tahoensis*). Hesslein et al. (1993) found liver $\delta^{13}C$ and $\delta^{34}S$ to be -4.1 ± 0.3‰ and -4.4 ± 0.4‰, respectively, relative to muscle, in growing broad whitefish. Other researchers have found differences between eggs and muscle in fish (Bilby et al. 1996, McCarthy and Waldron 2000, Grey 2001), while an assortment of tissues have been compared in other aquatic species with various results (Hobson et al. 1996, Gorokhova and Hansson 1999, Pinnegar and Polunin 1999, McCarthy and Waldron 2000, Lorrain et al. 2002). It is, therefore, recommended that a variety of individuals and tissues be analyzed to accurately reflect the overall consumption pattern and fractionation effects for a group of study animals, particularly those captured in the field.

Nutritional status

The nutritional status of animals collected in the field can have a strong influence on tissue isotope ratios. Hobson et al. (1993) demonstrated ^{15}N enrichment in Japanese quail muscle, liver, bone, and blood after 17 days rearing on a diet designed to maintain, but not increase, body weight. This experiment was an attempt to model conditions encountered during fasting, and was supported by ^{15}N enrichment in liver and muscle of female Ross geese (*Chen Rossi*) during egg laying and incubation, a period during which the bird consumes no food. Enrichment was also observed in crows that lost body mass during the course of an experiment (Hobson and Clark 1992a). The authors attributed the observed enrichments to either retention of enriched nitrogen for protein synthesis (i.e. excretion of depleted nitrogen, Mizutani and Wada 1988, Altabet and Small 1990), or discriminatory hydrolysis of amino acids with different $\delta^{15}N$ values (Gaebler et al. 1966).

Enrichment of salmon tissues following a period of fasting during the spawning migration (Doucett et al. 1999d) was attributed to isotopic fractionation associated with protein recycling (Macko et al. 1986). Tissues can also become ^{13}C-enriched during periods of food deprivation (Haines and Montague 1979) due to the respiration of isotopically light CO_2 (DeNiro and Epstein 1978, Perkins and Speakman 2001). Other workers, however, have found no effect of fasting on stable isotope ratios (larval krill, Frazer et al. 1997, mysids, Gorokhova and Hansson 1999, red drum larvae, Herzka and Holt 2000).

Age

The effect of age on tissue isotope ratios has received some attention. No influence of age on $\delta^{15}N$ was found in marine mussels (Minagawa and Wada 1984) or lake trout (Kiriluk et al. 1995). However, Overmann and Parrish (2001) found that 81% of variation in walleye (*Stizostedion vitreum*) $\delta^{15}N$ was accounted for by age, with diet

having little effect, and cod (*Gadus morhua*) otolith $\delta^{13}C$ has also been shown to increase with age (Schwarcz et al. 1998).

CONCLUSION

The use of SIA as an analytical technique is becoming more widespread and further research can only help in fully understanding the processes responsible for observable differences in the atomic composition of living and non-living things. The advantage of SIA over conventional techniques is in its allowance for non-lethal sampling, and the integrative picture of short- or long-term diet/metabolism it provides. It has become a valuable tool that when coupled with dietary information helps establish food web interactions and energy flow in various ecosystems.

The observed deviations from established patterns in stable isotope ecology are a reminder of the importance of variations and unpredictability in biological systems, but they by no means prevent the effective use of stable isotopes in field and lab studies. Instead, they require the researcher's awareness of potentially misleading observations in interpretation of stable isotope data.

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APPENDIX I

Stable Isotope Laboratories in Canada (from geology.uvm.edu/isogeochem.html, with contact information where available)

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British Columbia

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Manitoba

The University of Winnipeg Isotope Laboratory
www.uwinnipeg.ca/~geograph/CF-IRMS/UWIC.htm

Ontario

Environmental Isotope Laboratory
Department of Earth Sciences
University of Waterloo
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Sciborg.uwaterloo.ca/research_groups/eilab

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601 Booth Street
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Saskatchewan

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